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PSYCHE

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SOME NEW WEST INDIAN EUMOLPID BEETLES

By Doris H. Blake

This paper is made up of the descriptions of six new species of *Metachroma* and a new species of *Chalcosicya*. Four of the seven new species were collected by Fernando de Zayas, who has been actively collecting insects in Cuba over many years. One of the other species was taken by Dr. J. F. G. Clarke on the Breden Smithsonian expedition in 1956 and the two others are from miscellaneous material in the National Museum collection.

Chalcosicya alayoi new species

Figure 1

About 4 mm. in length, broadly oblong oval, shining, densely and coarsely punctate and with white pubescence not obscuring surface, black, except the brownish mouthparts, tibiae and tarsi.

Head with wide flat interocular space having a slight depression on vertex, densely and coarsely punctate and with long, closely appressed, white pubescence not concealing the shiny black surface below; mouthparts brownish. Antennae slender, not reaching the middle of the elytra, reddish brown. Prothorax convex, well rounded over head, sides arcuate, projecting in a sharp tooth beside eye, surface shiny, densely and coarsely punctate, and with long white pubescence. Scutellum rounded, shiny. Elytra broad, convex, a little prolonged at apex but not so conspicuously so as in many species of *Chalcosicya*, as *C. crotonis* Fabr. and *C. maestrensis* Blake; humeri well marked, a short depression within and another below basal callosity, surface very shiny and with coarse punctures, denser in basal depression, and rather sparse semi-erect white pubescence interspersed with finer pale brown erectish hairs. Body beneath shiny black, coarsely punctate, and with white pubescence. Anterior femora toothed. Length 4.3 mm.; width 2.6 mm.

Type, male, U.S.N.M. Type No. 64531, from Ciudamar, Oriente Province, Cuba, collected in July 1953 by Fernando de Zayas and Pastor Alayo. One other specimen, a female, from Daiquiri, Oriente Province, collected in March 1955 by Zayas.

Remarks. — There are several species of *Chalcosicya* in Cuba, but this differs from C. *maestrensis, rotunda,* and *nana* by having the anterior femora toothed, from *C. parsoni* in being black, not green, from *ditrichota* in its more rounded form and differently shaped aedeagus. The second specimen from Daiquiri, in Zayas' collection, is a female, but I believe the same species.

Metachroma zayasi new species

Figure 2

About 4.5 mm. in length, broadly oblong oval, lustrous black with the antennae, tarsi and body beneath deep brown; the elytra with the striate punctation most developed in area about basal callosity and becoming faint at base and after the middle of the elytra.

Head with interocular space about one-third width of head, occiput finely punctate, a short median line down vertex and the usual groove about inner margin of eyes, lower front more densely and coarsely punctate; head shining above and becoming alutaceous in lower front, the mouthparts deep brown. Antennae not extending to the middle of the elytra, the outer joints slightly wider than the basal, deep brown. Prothorax nearly twice as wide as long at its widest with arcuate sides, convex, lustrous, finely punctate. Scutellum deep brown. Elytra lustrous black, the striate punctation not very distinct over basal callosity but becoming large in depression below and in intrahumeral sulcus, then becoming indistinct after the middle of the elytra. Body beneath shining deep brown or piceous with the tarsal joints paler brown. Length 4.5 mm; width 2.5 mm.

Type, male, U.S.N.M. No. 64536, from Sierra del Cristal, Oriente Province, Cuba, collected in May 1955 by Fernando de Zayas.

Remarks. — This differs from *Metachroma schwarzi* Blake in being less coarsely punctate. In all the catalogues *Metachroma* is treated as a feminine noun and the specific names have the feminine ending, but in both Latin and Greek the word is neuter and the specific endings should be neuter.

Metachroma cornutum new species

Figure 3

About 3.5 mm. in length, broadly oblong oval, shining, the elytra with a few short rows of striate punctures in basal half, reddish brown, the seven distal joints of antennae dark, lower front of head with a conspicuous outgrowth on each side forming two horns.

Head reddish brown, the interocular space about half its width; smooth over occiput and down front, with the usual groove about inner margin of eyes; at base of lower front above labrum on each side a small knob that projects outward when looked upon from above; jaws large and brown tipped. Antennae not reaching the middle of elytra, with the three basal joints pale yellowish brown, the rest gradually deepening in color. Prothorax about one-third wider than long with rounded sides and a small tooth at apical and basal angles; fairly convex, mirror smooth, entirely reddish brown. Scutellum reddish brown. Elytra short, broad and moderately convex with a distinct intrahumeral sulcus marked by a row of striate punctures vanishing before the middle, below the basal callosity four other short rows of punctures, a subsutural depressed line with punctures about the scutellum. Body beneath shining reddish brown with abdomen and legs a little paler. Middle and posterior tibiae emarginate near apex, claws long. Length 3.5 mm.; width 1.8 mm.

Type, male, U.S.N.M. Type No. 64532, collected by E. A. Schwarz October 5, at Cayamas, Cuba.

Remarks. — The very unusual development of the lower front of face with two hornlike excrescences marks this species. Unfortunately only one specimen is known.

Metachroma bredeni new species

Figure 4

About 4 mm. in length, broadly oblong oval, shining, entirely yellowish brown, the prothorax alutaceous, the elytra distinctly striate punctate to below the middle.

Head with interocular space a little less than half width of head, occiput rounded, smoothly alutaceous with faint fine punctures, frontal tubercles outlined by a short median line down vertex, and a transverse line between eyes, the usual deep groove about inner margin of eyes; lower front alutaceous, not at all shiny, head entirely dull reddish brown with the jaws deep brown. Antennae extending nearly to the middle of elytra, the basal six joints paler and narrower than the outer joints. Prothorax not quite twice as broad as long with arcuate sides and a small sharp tooth at each angle, a short transverse depression over occiput, otherwise moderately convex, alutaceous and finely punctate, entirely pale yellowish brown. Scutellum pale. Elytra with a short intrahumeral sulcus and slight transverse depression below basal callosity; regular and well defined rows of punctures to beyond the middle of the elytra, the rows then becoming faint and indistinct on sides and apex; surface shiny, pale yellowish brown. Body beneath entirely pale, legs pale, femora obsoletely punctate at apex, the usual emargination near apex of middle and posterior tibiae. Length 4 mm.: width 2.2 mm.

Type, female, U.S.N.M. Type No. 64533, collected by J. F. G. Clarke on the Breden Smithsonian expedition, March 21, 1956, at Castle Bruce Junction, Dominica, B.W.I.

Remarks. — The entirely pale color and well marked striate punctation differentiate this from other pale West

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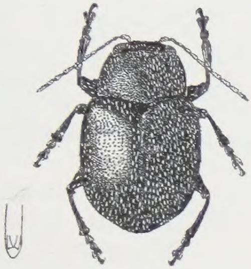
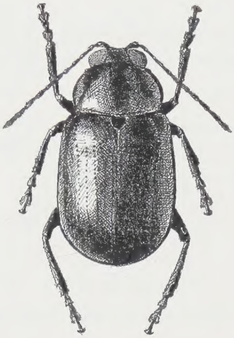
EXPLANATION OF PLATE 11

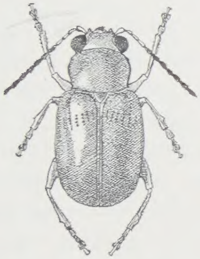
Figures 1-7. Fig. 1, *Chalcosicya alayoi,* Type, from Ciudamar, Oriente Prov., Cuba. Fig. 2, *Metachroma zayasi,* Type, from Sierra del Cristal, Oriente Prov., Cuba. Fig. 3, *Metachroma cornutum*, Type, from Cayamas, Cuba. Fig. 4, *Metachroma bredeni,* Type, from Dominica, British West Indies. Fig. 5, *Metachroma nanum,* Type, from Puerto Rico. Fig. 6, *Metachroma multipunctatum,* Type, from Sierra del Cristal, Cuba. Fig. 7, *Metachroma grande,* Type, from Yunque, Oriente Prov., Cuba.



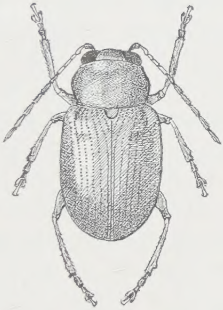
1. Chalcosicya alayoi



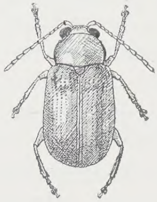
2. Metachroma zayasi



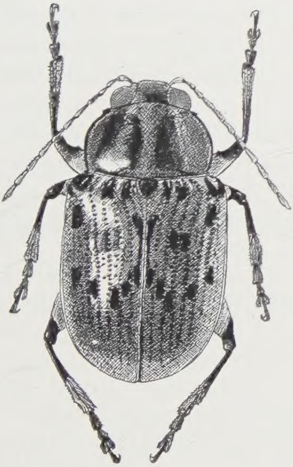
3. Metachroma cornutum



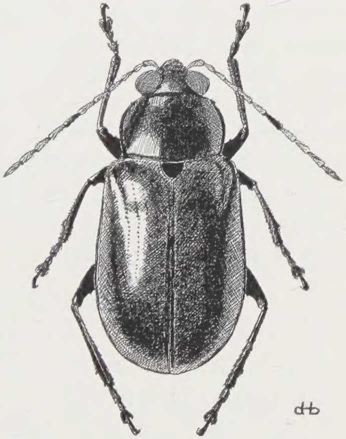
4. Metachroma bredeni



5. Metachroma nanum



6. Metachroma multipunctatum



7. Metachroma grande

BLAKE — EUMOLPID BEETLES

Indian species. It is the first species of *Metachroma* to be described from Dominica. It resembles several North American species of *Metachroma* (such as *M. pallidum* Say) but has a less coarsely punctate head and prothorax, and in those species the prothorax is usually a deeper reddish brown in color.

Metachroma nanum new species

Figure 5

About 3 mm. in length, oblong oval, shining, the elytra distinctly striate punctate, yellow brown without darker markings except brownish mouthparts.

Head with interocular space half its width, lightly but densely punctate over occiput, a groove about inner margin of eyes and a transverse line between antennal sockets; jaws large and deeper brown in color. Antennae entirely pale, not extending to the middle of the elytra. Prothorax moderately convex with arcuate sides, surface shining, very indistinctly punctate, entirely pale. Elytra with intrahumeral sulcus accentuated by row of punctures, and the depression below basal callosity having coarser punctures there, the striate punctation becoming gradually finer and evanescent at apex; surface very shiny, entirely pale yellow brown. Body and legs entirely pale, the usual emargination near apex of middle and hind tibiae. Length 3 mm.; width 1.6 mm.

Type, female, U.S.N.M. Type No. 64534, collected by Kline on guava (*Psidium guajava*), May 31, 1951, in Puerto Rico.

Remarks. — This is approximately the size of the Cuban species, *M. lituratum* Suffrian, but lacks the dark markings, and is also more distinctly punctate on the elytra.

Metachroma multipunctatum new species

Figure 6

Between 5.5 and 6.5 mm. in length, broadly oblong oval, very shiny, the pronotum finely punctate, the elytra with large, closely set, striate punctures throughout; two of the four specimens deep chocolate brown with a large piceous spot on either side of pronotum and a row of three dark spots across the base of each elytron and one below the humerus and another in middle below that and an irregular row of four below middle; suture in part dark; in the other two specimens the pronotum and elytra entirely dark; femora dark at apex, tibiae dark at base, entirely dark in dark specimens.

Head with interocular space about one-third width of head; coarsely and shallowly punctate, more densely so in lower front, a short median line and the usual deep groove along inner margin of eyes; deep brown or piceous. Antennae reddish brown, not reaching the middle of the elytra. Prothorax not quite twice as wide as long at widest point, with arcuate sides and small tooth at each angle, a transverse depression over occiput anteriorly; surface lustrous, finely and not densely punctate, in pale specimens a deep reddish brown with a large dark spot nearly covering each side, leaving only a small area anteriorly and at base and a median line pale, in dark specimens entirely dark. Scutellum piceous. Elytra broad and moderately convex with only a short intrahumeral sulcus, very coarsely striate punctate with some irregular punctures between the rows at the middle, punctation deep and distinct on the sides and at apex; very shiny, deep brown with darker spots consisting of three across the base of each elytron, one below humerus, another in middle and in a row of four below the middle, suture in part dark. In dark specimens the elytra entirely dark. Body beneath dark in all specimens, the femora in paler specimens pale with dark apex, the tibiae dark in basal half; in dark specimens the legs entirely dark; the usual emargination near apex of middle and hind tibiae. The front and hind femora with a small tooth. Length 5.5 to 6.5 mm.; width 3 to 3.7 mm.

Type, female, U.S.N.M. Type No. 64535, and three paratypes, all females, one of these in the collection of F. de Zayas, all collected in the Sierra del Cristal, Oriente Province, Cuba, May 1955, by F. de Zayas.

Remarks. — Although I have examined no males, I believe that these specimens represent two color forms, as in *M. longitarsum* Blake, one pale with spots, and the other entirely dark. The large, closely placed punctures serve to distinguish this species. The type is of the spotted form.

Metachroma grande new species
Figure 7

About 6.5 mm. in length, broadly oblong oval, shining, the occiput and prothorax very lightly punctate, elytra with striate punctures also very light except in depression below basal callosity, entirely deep piceous black except the reddish brown antennae, tarsal joints and head.

Head with interocular space considerably less than half the width of head, eyes large, vertex with median line, as well as deep groove around the inner margin of eyes, surface finely and not densely punctate, lower front wrinkled; mouthparts paler reddish brown than the rest of head which is deeper brown. Antennae reddish brown, the 7th joint deeper brown, slender, not reaching middle of elytra. Prothorax not twice as broad as long, moderately convex, with rounded sides and small acute tooth at each angle, a slight transverse depression over head, surface very shiny and with fine, scarcely discernible punctures, entirely piceous. Scutellum piceous. Elytra with an intrahumeral sulcus and a depression below basal callosity with the striate punctures larger in depression and thence becoming finer and at sides and apex almost vanishing; surface lustrous piceous black. Body beneath and legs piceous, the tibiae at apex and tarsal joints deep reddish brown; the usual emargination near apex of middle and hind tibiae, and the front and hind femora with a small tooth. Length 6.5 mm.; width 3.2 mm.

Type, female, from Yunque, Oriente Province, Cuba, collected in July 1955 by F. de Zayas, and in his collection.

Remarks. — This is larger than either *M. zayasi* or *M. schwarzi* Blake and also less coarsely punctate on the elytra.

CEPHALIC GLANDS IN *GELASTOCORIS* (HEMIPTERA-HETEROPTERA)

By Margaret C. Parsons[1]

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In the literature on the anatomy of the aquatic Cryptocerata (Hemiptera-Heteroptera) there are many references to the "cephalic" or "maxillary" glands. These large cylindrical or sac-like structures, whose external openings lie at the base of the labium, are located on either side of the head in the Corixidae (Banks, 1939; Benwitz, 1956), Notonectidae (Bordas, 1905 a; Bugnion and Popoff, 1908), Naucoridae (Becker, 1929; Rawat, 1939), and Belostomatidae (Locy, 1884; Bugnion and Popoff, 1908). In the Nepidae, they may be partly (*Nepa*; Bordas, 1905 b) or entirely (*Ranatra*; Bugnion and Popoff. 1908; Neiswander, 1925) contained in the thorax, with ducts leading to the openings in the head. Previous investigations of these glands in the Cryptocerata have mentioned their presence only in the aquatic forms; they have never been reported in the shore-dwelling cryptocerates.

While studying the anatomy of the shore-dwelling cryptocerate *Gelastocoris oculatus oculatus* (Fabricius) (Gelastocoridae), the author noted two large, sac-like structures, one lying on either side of the ventral part of the head. Figure 1 indicates, in dotted lines, their approximate position, which is revealed by cutting away the exoskeleton from the entire ventral surface of the head. They lie immediaetly beneath this exoskeleton, extending anteriorly to the base of the labium and posteriorly a little beyond the antennal socket. Anteriorly they reach nearly to the

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[1] This research was carried out during the tenure of the Ellen C. Sabin Fellowship, awarded by the American Association of University Women. Thanks are due to the members of the C. V. Riley Entomological Society, Columbia, Missouri, who collected the specimens of *Gelastocoris*.

midline, but diverge from each other posteriorly in the region of the subesophageal ganglion. They are bordered dorsally by the mandibular lever and the retractor muscles of the mandibular and maxillary stylets, and laterally by the sides of the head. The fact that these structures contain copious amounts of a milky secretion, and that their lumina open through definite orifices, suggests that they are glandular in nature. When the bug is disturbed, large quantities of this secretion are emitted from the large orifices, which are located on the ventral surface of the head just anterior to the antennal sockets (Fig. 1). In the following discussion, the term "orifice" will refer only to the hole in the exoskeleton, while the mouth of the gland, lying beneath the orifice, will be termed the "glandular opening."

The opening mechanism of the gland is controlled by a slender muscle, which originates on the tip of the posterior wing of the hypopharynx and runs ventral to the gland to insert on a flap on the medial side of the glandular opening (Fig. 4). This flap is sclerotized and elastic; its two

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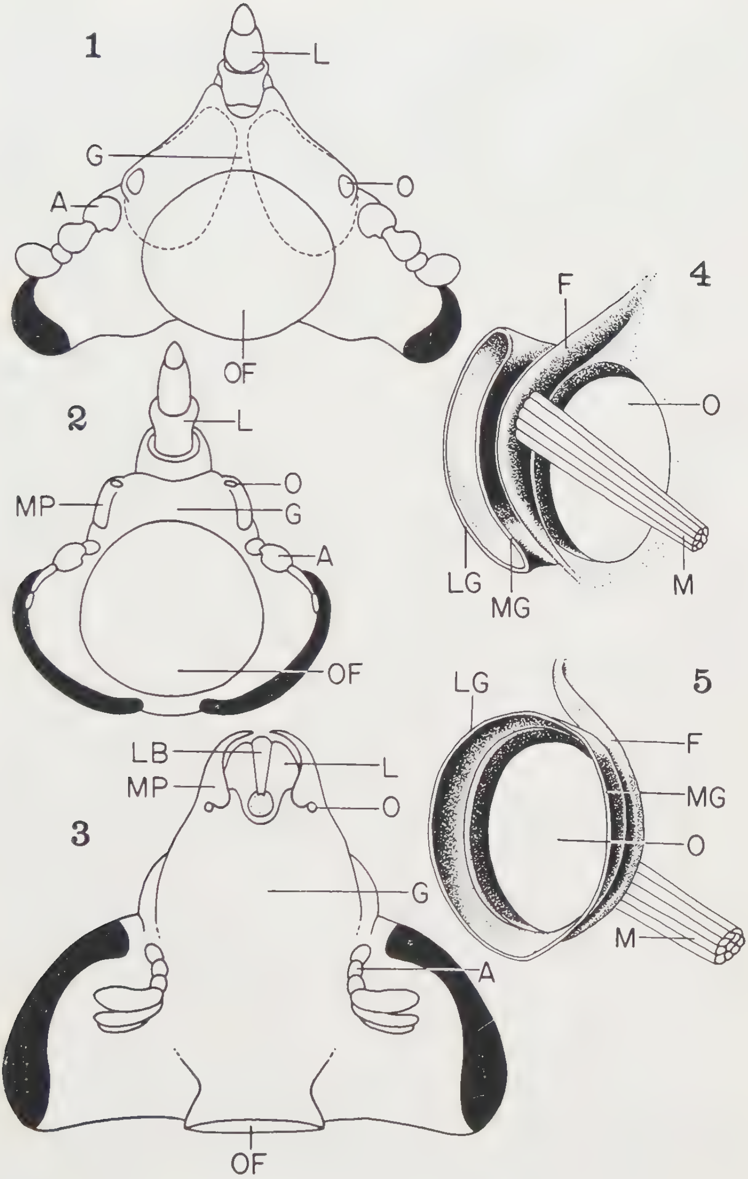
Explanation of Plate 12

Figures 1-3. Ventral views of the heads of representative Cryptocerata, showing the positions of the orifices of the cephalic glands. The eyes are colored solid black. Figure 1. *Gelastocoris oculatus oculatus.* The dotted lines indicate the approximate position of the cephalic glands inside the head. 20 X. Figure 2. *Notonecta undulata.* 10 X. Figure 3. *Belostoma flumineum.* The labrum and labium have been cut off at the base of the second labial segment. 13 X. Figures 4 and 5. Views of the inner ventral surface of the head of *Gelastocoris,* showing the opening mechanism of the left cephalic gland. The anterior direction is to the top, the posterior direction to the bottom, the lateral direction to the left, and the medial direction to the right of the diagram. 375 X. Figure 4. The muscle is relaxed, and the glandular opening is shut off from the orifice in the exoskeleton. Figure 5. The muscle is contracted, and the glandular opening is pulled over beneath the orifice.

Abbreviations Used in Plate: A — antenna; F — sclerotized flap on medial side of glandular opening; G — gula; L — labium; LG — lateral wall of glandular opening; LB — labrum; M — muscle inserting on sclerotized flap; MG — medial wall of glandular opening; MP — maxillary plate; O — orifice in exoskeleton of head; OF — occipital foramen.



Parsons — Cryptocerata

ends are fused to the exoskeleton of the head on either side of the orifice, while its middle part is connected to the medial side of the glandular opening. When the muscle is relaxed, the flap lies just beneath the lateral edge of the orifice, and thus separates the orifice, which lies medial to it, from the glandular opening, which is lateral to it (Fig. 4). When the muscle contracts, the flap is pulled over to just beneath the medial side of the orifice; the glandular opening then lies immediately below the orifice, and the secretion can escape through the latter (Fig. 5).

The wall of the gland is very smooth and delicate, and appears silvery in freshly dissected specimens. Its histology was examined in serial sections through the heads of two fifth-instar nymphs and three adults of *Gelastocoris;* the material was fixed in Carnoy's or alcoholic Bouin's, prepared for sectioning by means of the Peterfi method, and stained in either Mallory's triple connective-tissue stain or in Delafield's hematoxylin and eosin. Text-figure 1 shows the general appearance of the glandular epithelium in an adult specimen. It is comprised of a simple layer of cells with no suggestion of an acinar arrangement. The most conspicuous elements are the large cells, which are usually flat in adult gelastocorids but appear more cubiodal or cylindrical in the nymphs. These cells probably produce the secretion. Their large nuclei are about 15 μ in diameter, and contain conspicuous nucleoli and many chromatin granules of various sizes. The cytoplasm is homogeneous and deeply staining in adults but appears more vacuolar in nymphs. An intracellular canaliculus with striated walls penetrates the cytoplasm of each large cell; it seems to run across the cell in an obliquely transverse direction, opening onto the lumen of the gland usually near the lateral boundary of the cell.

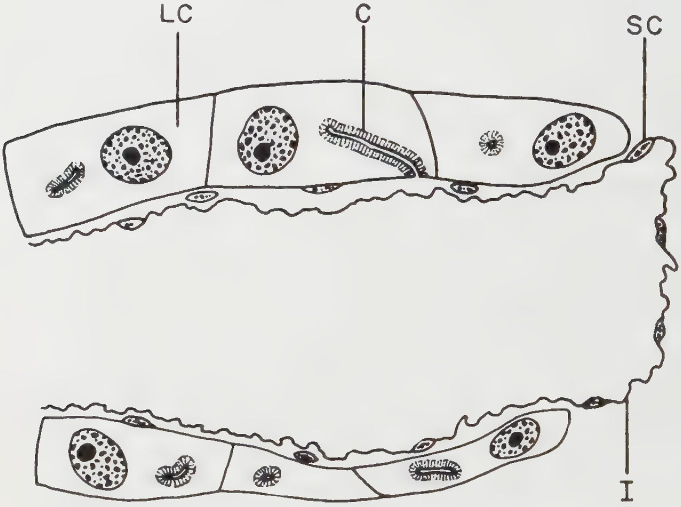
The lumen of the gland is lined by a delicate chitinous intima, which does not appear to penetrate into the canaliculi. Lying along the intima or between the intima and the large cells are small spindle-shaped nuclei, whose cytoplasm is either very sparse or absent; their greatest diameter ranges between 5 and 10 μ. In many parts of the epithelium the large cells are absent, and only the intima and the small nuclei remain. Such regions are not confined to any definite area of the gland, and their location varies from one individual to the next. The epithelium is never more than 15 or 20 μ thick, and the bulk of the gland consists merely of the very extensive lumen filled with a homogeneous, finely granular secretion which stains blue in Mallory's triple connective-tissue stain and pink in Delafield's hematoxylin and eosin.

These glands in the Gelastocoridae resemble in several ways the cephalic glands of aquatic Cryptocerata, and the similarities suggest that the former are homologous with the latter. Their paired ventral position in the head corresponds to that described by other authors for the cephalic glands of the Notonectidae, Naucoridae, Belostomatidae, and Corixidae (in the last family only the anterior part of the gland is ventral, the posterior part being dorsal to the brain). The simple sac-like shape of the gelastocorid glands is consistent with the previous descriptions of cephalic glands in aquatic bugs; to the author's knowledge, only the Naucoridae show a more complicated structure, having a lobed reservoir beside the glandular part of each gland (Becker, 1929; Rawat, 1939). A muscle controlling the opening mechanism of the gland has been described in *Corixa* and *Notonecta* (Benwitz, 1956) and in *Naucoris* (Becker, 1929); although in the former two genera this muscle originates on the wall of the head, in *Naucoris* it is attached, like that of *Gelastocoris,* to the tip of the posterior wing of the hypopharynx.

Histologically there are further resemblances. The three main components, the large cells, the smaller cells, and the chitinous intima, are mentioned in *Corixa* (Benwitz, 1956), *Naucoris* (Rawat, 1939), *Ranatra* (Bugnion and Popoff, 1908), and *Notonecta* (Bordas, 1905 a). The secretory epithelium is reported to be arranged into acini in *Naucoris* (Becker, 1929; Rawat, 1939) and *Notonecta* (Bugnion and Popoff, 1908), but no such arrangement is mentioned for the other forms. Locy (1884), Bugnion and Popoff (1908), and Benwitz (1956) report intracellular canaliculi within the large cells, similar to those seen in

Gelastocoris, and the last author describes the striations along these canaliculi.

The main difference between the glands of *Gelastocoris* and those of the aquatic Hemiptera is in the position of their external openings. Whereas in the aquatic Cryptocerata the orifices lie at or near the base of the labium, in *Gelastocoris* they are located much farther posteriorly on the head. A comparison of Figure 1 with Figures 2 and 3 points out this difference; *Notonecta undulata* and *Belostoma flumineum* are used as representatives of the aquatic forms.



Text-figure 1. Diagrammatic transverse or longitudinal section through the epithelium of the cephalic gland in an adult *Gelastocoris.* In this diagram the epithelium is folded double, so that the lumen appears much narrower than it actually is. The canaliculus of the upper middle large cell is shown opening onto the lumen of the gland; the other canaliculi are diagrammed in transverse or oblique section. 700 X.

Abbreviations used in figure: C — canaliculus; I — intima; LC — large cell; SC — small cell.

The function of the cephalic glands in the water bugs has not yet been satisfactorily established. Previous workers have suggested (1) that their secretion is used in subduing prey, being somehow injected into or ingested by their victims, (2) that the secretion is defensive, serving to repel predators, or (3) that the glands function as excretory organs. The last theory was proposed by Becker (1929), but it was attacked by Rawat (1939) who found that carmine injected into the head of *Naucoris* was not taken up by the glands; the first two theories appear to be the most popular. In *Gelastocoris* it is unlikely that the secretion of the cephalic glands could be used for killing or paralyzing prey, since the orifice is a good distance from the beak. It seems most probable that it has a defensive function.

To the author's knowledge, cephalic glands have been reported in only three Gymnocerata. Macgill (1947) gave a brief description of two groups of glandular cells in the phytophagous bug *Dysdercus* (Pyrrhocoridae). These cells lie near the stylets and open onto the anterior part of the maxillary plate, at the base of the labium, by many small pores. Macgill considered their function to be the lubrication of the stylets; no histological details were given. Bugnion and Popoff (1911) figured maxillary glands in a section through the head of *Pyrrhocoris* (Pyrrhocoridae), but gave no histological description and did not mention the position of the external orifice. A brief account of maxillary glands in *Oncopeltus* (Lygaeidae) was given by Linder and Anderson (1955). It seems therefore that the cephalic glands are characteristic of the Cryptocerata but occur in the Gymnocerata. According to China (1955), the shore-dwelling families Gelastocoridae and Ochteridae are the most primitive of the Cryptocerata, having diverged from the ancestral line before it became aquatic. To date, however, the relationships between the aquatic and shore-dwelling Cryptocerata have been hypothesized mainly on the basis of external structural characters. The presence of cryptocerate-like cephalic glands in *Gelastocoris* offers some evidence from internal morphology that the Gelastocoridae are closely related to the aquatic Cryptocerata.

It might be proposed, on the basis of China's evolutionary theory, that the position of the orifice in *Gelastocoris* is the primitive condition, while that seen in the aquatic bugs is a specialization, possibly accompanying a partial or total shift in glandular function from a defensive organ to a poison gland. Since, in all the aquatic bugs studied, the orifice is always near the base of the beak, bordering on the maxillary plate (Benwitz, 1956), any change to this location from that seen in *Gelastocoris* would have to have occurred just before the primitive line diverged into separate aquatic families. Against this theory, however, is Macgill's observation that the opening of the glands in the gymnocerate *Dysdercus* are at the base of the labium. This suggests that this location of the orifice is the primitive condition, and was found in the Proto-Heteroptera (to use the term of China, 1955) before the Gymnocerata and Cryptocerata diverged. If this theory is correct, the more posterior position of the orifice in *Gelastocoris* is a secondary acquisition. Why such a shift should take place is not clear, however, since the gelastocorids are predators, like their aquatic relatives, and orifices associated with the labium, which could allow the glands to serve as poison glands, would be advantageous to them. Although the second of these theories appears at this time to be the more commendable, more information on the presence or absence of cephalic glands in other Heteroptera, and on the location of their orifices, is needed to shed further light on this problem.

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CHEMICAL RELEASERS OF NECROPHORIC BEHAVIOR IN ANTS

By E. O. Wilson,[1] N. I. Durlach,[2] and L. M. Roth[3]

Introduction

One of the more conspicuous and stereotyped patterns of social behavior exhibited by ants is the transport of dead members of the colony from the nest to the refuse piles (McCook, 1882; Wheeler, 1926). Because of the obvious simplicity of this "necrophoric" response and the ease with which it can be experimentally elicited, it has proven to be one of the forms of ant behavior most amenable to physiological analysis. In the present paper are presented the results of a preliminary study of the response in the myrmicine ants *Pogonomyrmex badius* (Latreille) and *Solenopsis saevissima* (Fr. Smith), in which special attention has been paid to the releasing stimuli.

Description of the Behavior

When the corpse of an adult *Pogonomyrmex badius* worker that has been allowed to decompose in the open air for a day or more is placed inside the nest or outside near the nest entrance, the first sister worker to encounter it ordinarily investigates it briefly by repeated antennal contact, then picks it up and carries it directly away from the nest toward the refuse piles. Under the conditions existing during the present study, most of the refuse piles of the captive colonies were located less than one meter from the nest entrance along the back wall of a closed foraging arena. This distance was evidently inadequate to allow the rapid consummation of the corpse removal response, for workers bearing corpses frequently wandered for many minutes back and forth along the back wall before dropping their burdens on the refuse piles. Others were seen to approach the back wall unburdened, to pick up corpses already on the piles, and to transport them in similarly restless fashion before re-depositing them.

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It is a curious fact that in nature such "cemeteries" are rare or non-existent in the vicinity of *Pogonomyrmex badius* nests. During field studies conducted in northern Florida and southern Alabama, it was found that corpses removed from the nests are carried only a short distance beyond the rim of the nest crater before being dropped. Once abandoned, they are soon collected by scavenging workers of the dolichoderine species *Conomyrma pyramica* (Roger), one of the dominant ants occurring with *P. badius* in its native range. The swift *Conomyrma* workers patrol the vicinity of the *Pogonomyrmex* nests in large numbers during the day, and their activities apparently prevent the accumulation of *Pogonomyrmex* dead. It is not known whether other ant species assume this role outside the range of *Conomyrma*.

In the laboratory most injured and dying *Pogonomyrmex badius* workers leave the nest interior before succumbing. These individuals are usually found wandering through the foraging arena, unattended by sister workers. If similar behavior is exhibited in nature, it can safely be inferred that the removal of corpses is thus accomplished in large part by the dying ants themselves, as their last act as living workers. Under laboratory conditions queens and some larger major workers remain within the nest while dying. Several times it was observed that the bodies of these individuals remained in the nest for three days, during which they were frequently licked and moved about by the workers. After that time they were removed to the refuse piles.

EXPERIMENTS

Assay of decomposition products. The following experiment was designed to determine whether certain substances separated from the body of the corpse could by themselves elicit necrophoric behavior. A square of filter paper six millimeters on the side was daubed with an acetone extract of *Pogonomyrmex badius* worker corpses and placed, in company with five untreated control squares, inside the foraging arena five centimeters from the nest entrance. In three separate trials, the treated squares were picked up within five minutes by the first workers to encounter them and transported directly to the refuse piles. In their reaction to the treated squares and in their locomotory patterns during transport, the workers appeared to behave in the same fashion as toward worker corpses. No immediate reaction to the control squares was noted, and they were not moved significantly from their original positions during the first several hours. In only one case was a control square transported in the direction of the refuse piles during the course of the first twenty-four hours.

A similar response was also evoked by objects other than paper squares. Seeds, for example, which ordinarily would be ignored or carried into the nest for storage, when daubed with the extract were carried to the refuse pile. The most dramatic example of the potency of this extract as a releaser occurred on three occasions when the objects chosen for experiment were live workers. Despite the fact that these ants were moving around under their own power and providing socially significant stimuli, they were treated by their sisters as corpses. However, unlike authentic corpses they would allow themselves to be carried to the refuse pile only to rise again and return to the nest! The cycle was observed to occur repeatedly during periods of one to two hours. During transport, the workers folded their appendages in the "pupal" posture usually taken by normal workers being carried to nest sites.

An attempt was next made to determine whether the chemical releasers could be removed from worker bodies by leaching so as to modify the response of living workers to the bodies. Three worker corpses were placed in bottles containing 50 cc. of acetone for periods of one to three weeks, then thoroughly dried and presented in succession to living workers in the manner described above. The behavior toward these treated bodies was markedly different from that shown toward untreated corpses. Instead of transporting them away from the nests, the workers began to lick and chew them vigorously. One was carried quickly *into* the nest; the other two were dragged back and forth for short distances near the nest entrance. Several untreated corpses placed around the leached bodies were at the same time carried directly off to the refuse piles. One of the leached bodies was recovered several minutes after its introduction, daubed with corpse extract, and reintroduced. The same workers that had been licking it previously now carried it directly to the refuse piles. The other two leached bodies were left in position to observe their subsequent treatment. One was dismembered by the living workers; both were carried away from the nests only after forty minutes or longer.

The paper-square test described previously was next employed to test a few common fat and protein decomposition products and related compounds obtained as chemical reagents. The following substances produced no detectable response, either in saturated or dilute solutions: ammonium sulfide, di-alpha-amine. Weak to moderate alarm behavior, followed occasionally by digging behavior[1], was evoked by the following substances: phenylethylamine, triethanolamine, phenol, n-valeric acid, n-caproic acid, n-caprylic acid, n-butyric acid, formic acid. The only substance tested that released the necrophoric response, or anything resembling it, was oleic acid. In repeated trials, oleic acid daubed onto paper squares and other small neutral objects invariably elicited a behavioral response from *P. badius* indistinguishable from that evoked by worker corpses.

On the assumption that oleic acid, or a related compound, is a principal natural releaser of the necrophoric response, an attempt was made to separate and analyze the long-chain fatty acids found in *Pogonomyrmex* worker corpses. Infrared spectra were prepared from a crude extract of about 200 dead bodies of *P. barbatus* (Fr. Smith). These spectra were made from a sample in CCl4 and from a liquid film after the carbon tetrachloride was evaporated.

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[1] A fuller account of alarm and digging behavior, and of the various stimuli that release these linked responses, has been presented elsewhere (Wilson, 1959).

The spectra indicated the presence in the crude extract of an ester (the principal compound) and a fatty acid. An attempt was made to separate the fatty acid from the mixture. The solvent of the original solution was evaporated and the residue dissolved in ether which was then washed with dilute Na_2CO_3. The alkaline wash containing the sodium salt of the fatty acid was separated from the ether solution containing the ester. The infrared spectrum of the ether solution compared well with the original crude material, indicating that the ester had been removed. The alkaline wash containing the Na salt of the fatty acid was acidified with dilute HCl and extracted with ether. The infrared spectrum of this ether extract indicated a fatty acid though the spectrum was not sufficiently distinctive to identify the compound specifically. In a series of tests using treated and untreated (control) paper squares, it was found that both the fatty acid and the ester evoked the necrophoric response. However, the fatty acid appeared to be the more effective of the two, in that it tended to release the response more quickly and to induce transport of the treated squares over greater distances. It was further observed that the acid-daubed squares were as a rule transported further away from the nest entrance during initial transport. Also, the ester-daubed squares frequently caused an initial mild alarm reaction that delayed the necrophoric response even more, whereas the acid-daubed squares were never observed to do so. It is possible that complete separation of the acid and ester was not obtained and that contamination of the ester fraction with the acid could account for the equivocal results.

Use of another test species. An attempt was next made to determine whether the fatty acid obtained from *Pogonomyrmex barbatus* would release necrophoric behavior in a phylogenetically remote ant species, *Solenopsis saevissima* (Fr. Smith). Four paper squares daubed with the acid were inserted, along with four control squares, into the brood chamber of an artificial nest containing a colony of *S. saevissima.* Within 25 minutes all four of the treated squares had been carried out and placed at the edge of the nest. Soon afterward the control squares were brought out and dropped at the same place. Five hours later all of the treated squares had been moved to a position about twenty centimeters beyond the nest edge. A *saevissima* worker was later seen carrying a treated square back and forth in the restless fashion commonly seen in workers of this species carrying corpses.

Assay of extract from another insect species. To determine whether fatty extracts of corpses of another insect species causes the necrophoric response in *Pogonomyrmex badius*, extracts from meal worms (*Tenebrio molitor*) allowed to decompose in open air for two weeks were tested in the usual fashion. Treated paper squares were carried promptly to the refuse piles by the *Pogonomyrmex* workers, whereas control squares were left untouched for the first several hours. The behavior of the ants toward the treated squares seemed identical to that shown toward squares treated with the extract of *Pogonomyrmex* corpses.

CONCLUSIONS

Pogonomyrmex badius workers utilize a relatively limited range of stimuli in "recognizing" insect corpses. Moreover, the stimuli appear to be exclusively chemical in nature. One of the principal chemical releasers is evidently the fatty acid that accumulates in the bodies of sister workers allowed to decompose in open air. An ester may also play a secondary role. Of several chemical compounds tested commonly found in insect corpses, oleic acid was the only substance which caused the ants to behave as they do toward dead insect bodies. Whether other substances present in ant corpses (and those of other animals) release the necrophoric response is not known. It may be suggestive that the common smaller molecular products of decomposition thus far tested have all produced neutral or alarm behavior without any element of necrophoresis. It is also noteworthy that long-chain fatty acids are chemically among the most stable and least volatile of fat and protein decomposition products and hence tend to accumulate disproportionately in insect corpses. As a result these substances have the potential to serve as efficient signals of the presence of aging corpses, as opposed to freshly killed and edible insect prey. Finally, the fact that the fatty acid from *Pogonomyrmex barbatus* corpses induced typical necrophoric behavior in both *P. badius* and *Solenopsis saevissima* workers suggests that this behavior and its natural releasers may be widespread in the ants.

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THE RELATIONSHIP OF THE PROTOPERLARIA AND THE ENDOPTERYGOTA

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The first worker to recognize that the Protoperlaria were a group distinct from the Protorthoptera, and probably ancestral to the Plecoptera, was Tillyard (1928a, b). The relationship of these orders has been discussed in more detail by Carpenter (1935). That the Protoperlaria might be of far greater phylogenetic significance has not generally been appreciated. Although the suggestion that the Protoperlaria were close to the ancestral form of the Endopterygota was made by Bradley (1939, 1942), this relationship has not previously been documented.

While a comparison was being made between the wings of the protoperlarian, *Lemmatophora,* and the neuropteran, *Sialis,* in an effort to determine the venational homologies of the latter, it became apparent that these insects exhibited a number of striking similarities. When the similarity of the wings was noticed, a comparison of other body structures seemed desirable. Since these could not be studied in the fossils, it was necessary to turn instead to the Plecoptera, in the hope that additional resemblances could be found. Such resemblances have been observed, particularly in the sternal region of the thorax, and in the wing articulation; these are discussed briefly below.

The Sialidae are extremely archaic insects; the venation has undergone but little change since the Permian. There are some specializations — fusion of MP and CuA in the fore wing, reduction of the anal fan, and lack of nygmata— but in structure and arrangement of the veins the wing remains primitive. No other living insect group shares with the Protoperlaria so many morphological features of the wing. *Sialis mohri* Ross has been used in this study; the other genera of this family differ only slightly. *Neohermes californicus* (Walker) (Corydalidae) has been used in the study of wing articulation, since the wing base is larger and apparently less specialized than in *Sialis.*

Material of *Lemmatophora typa* examined includes the neotype, M. C. Z No. 3536, which is almost perfectly preserved, and upon which Figures 3 and 4 are largely based. Of a long series of impressions of hind wings which were studied, M. C. Z. No. 4425 was best. In none of these fossil specimens were the extreme bases of MP and CuA preserved.

I should like to acknowledge the kindness of F. M. Carpenter, who has made available the material used in this study, and who, together with W. L. Brown and E. O. Wilson, has contributed many helpful suggestions.

A. STRUCTURE OF THE VEINS.

In *Sialis,* the veins are not heavily sclerotized, most of them being formed as longitudinal folds in the membrane (Fig. 9b). As a consequence, these veins appear, viewed from one surface, as ridges, and from the other surface, as grooves.

Since the fossil wings are molds of the upper and lower wing surfaces, it has been possible, by viewing under illumination nearly parallel to the surface, to reconstruct a cross-section of the hind wing of *Lemmatophora* (Fig. 9a). This is similar to that of *Sialis* in the general structure of the veins, and shares with it a remarkable peculiarity:

EXPLANATION OF PLATE 13

Figures 1, 2. *Sialis mohri* Ross. Anterior and posterior wings, showing venation and distribution of macrotrichia. Figures 3, 4. *Lemmatophora typa* Sellards. Anterior and posterior wings, showing venation and distribution of macrotrichia. Figure 5. *Pteronarcys californica* Newport. Portion of anal fan of posterior wing, showing macrotrichia on veins and membrane, and distribution of microtrichia. Figure 6. *Sialis mohri.* Structure of microtrichia and a macrotrichium. Figure 7. *Sialis mohri.* Portion of anterior wing, showing distribution of macrotrichia and microtrichia. (Microtrichia indicated by stippling.) Figure 8. *Lemmatophora typa.* Portion of anterior wing, showing distribution of macrotrichia and microtrichia. (Pigmentation indicated by stippling.)

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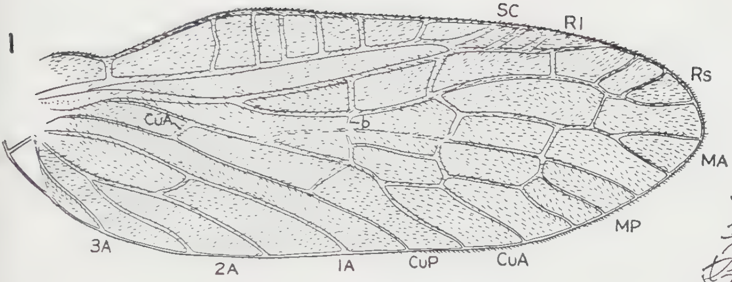

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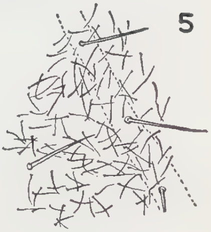

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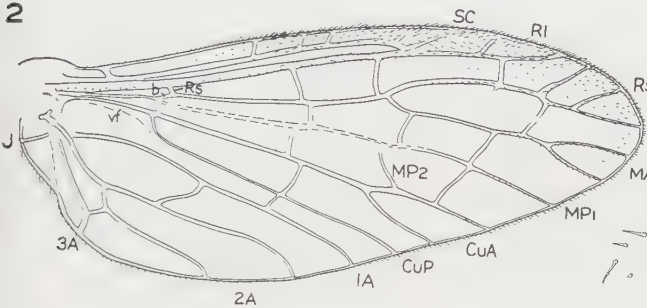

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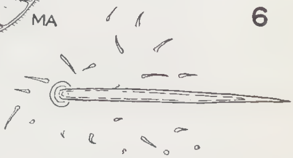

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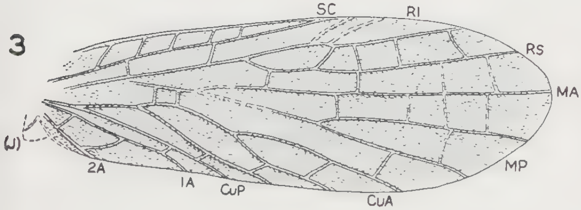

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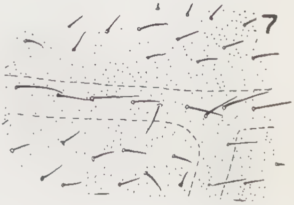

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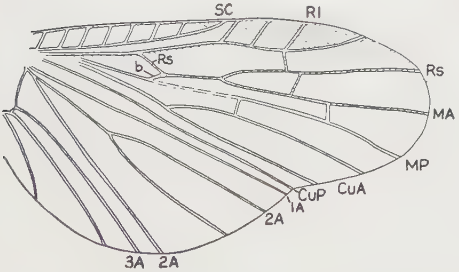

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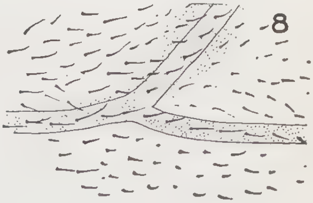


Adams — Protoperlaria and Endopterygota

CuA is formed like a trough, appearing as a deep groove when viewed from above, and as a strong ridge, viewed from below. While in *Lemmatophora,* CuA is still found in its primitive position, lying on a weak convex fold of the wing, in *Sialis* this fold has been reversed, so that CuA lies at the bottom of a concave fold. CuA in the hind wing of all the other Exopterygota I have examined, with the possible exception of the Caloneurodea, is either indeterminate or on a more or less convex fold as in *Lemmatophora.* In all the neuropteroids where CuA is well developed in the hind wing, it is on a concave fold, as in *Sialis.*

Another peculiarity of the Protoperlaria is the structure of the stem of MP, which frequently is so weak as to be nearly indiscernible. There is little differentiation of the wing membrane along the course of this vein, except for the occurrence of a row of macrotrichia, and its being surrounded by a non-pigmented area. In both wings of *Sialis,* the stem of MP has a similar structure. This condition is a most unusual one, and its occurrence in *Sialis* is of considerable significance.

B. VENATIONAL PATTERN

The arrangement of veins is fundamentally the same in *Sialis* and in protoperlarians. In *Lemmatophora* Rs is simple, but is 2- or 3- branched in some other members of this order. Rs in sialids also is simple, but for a few marginal veinlets. Fusion of MA with Rs is of frequent occurrence among protoperlaria, but is subject to much variation. In *Lemmatophora,* coalescence of these two veins is clear in the posterior wing, as in the hind wing of *Sialis.* In the fore wing of *Lemmatophora,* coalescence does not take place. In *Sialis* it has, although the connection between MA and the base of MP is not clear as in the hind wing; here a weak crossvein may represent the basal piece of MA, or the basal piece may have moved toward the wing base and disappeared. The basal piece is, however, readily identifiable in the fore wings of most primitive Raphidiodea and Planipennia.

Fusion of CuA and MP in the fore wing, characteristic of Sialidae and Archisialidae, also occurs in some Protoperlaria (*Leucorium, Artinska*), but is not ordinarily found among the Planipennia.

Probably the most striking difference between the wings of *Lemmatophora* and *Sialis* lies in the shape, there being a well-developed anal fan in the protoperlarian, but none in *Sialis*. However, a functional fan is still present in the Corydalidae, and a reduced one in the Ithonidae and Polystoechotidae. Anal fans occur elsewhere in the Endopterygota, notably in the Trichoptera and Lepidoptera; one would therefore expect such a structure to be present in the ancestor of the Endopterygota. That its absence in *Sialis* is due to secondary reduction is indicated by the still relatively broad base of the hind wing. Reduction of the anal fan in *Sialis* is compatible with a general trend in the Neuroptera toward narrowing of the base of the hind wing.

C. TRICHIATION OF THE WINGS AND VEINS

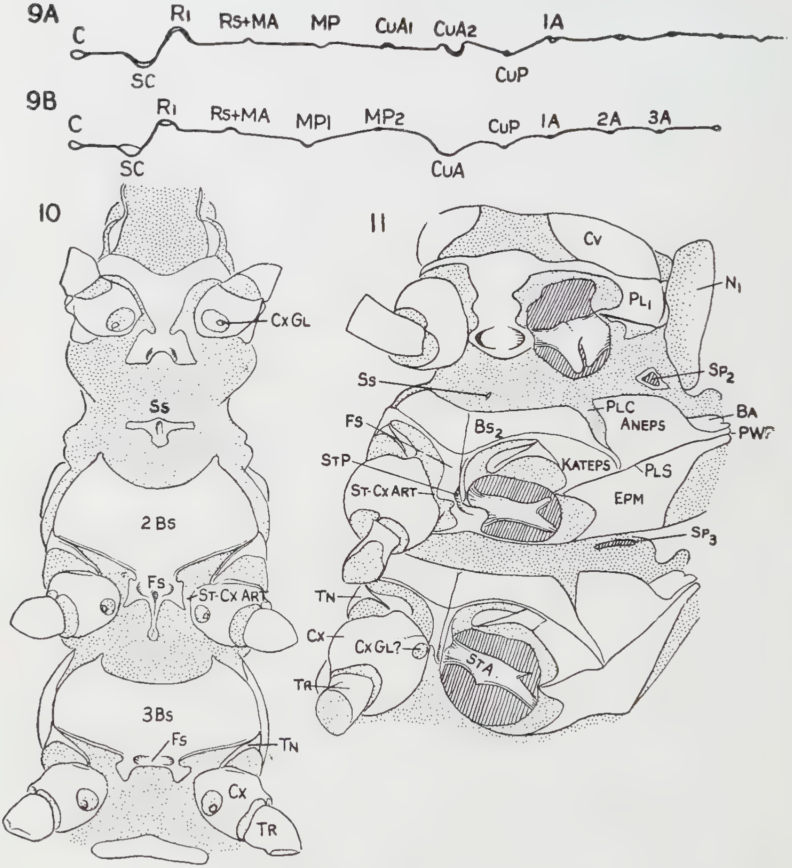
Tillyard (1918) has discussed the trichiation of the wings in the Panorpoid Orders; he distinguishes two types of hairlike structures — *macrotrichia,* with articulated bases, equivalent to setae, and *microtrichia* which are simple outgrowths of the cuticle. Macrotrichia are found both on the veins and the wing membrane in many Endopterygota, but among the Exopterygota are largely restricted to the veins. Microtrichia occur in both groups, distributed uniformly over the surface of the wing, including the veins.

Tillyard (1928a) interpreted the fine hairs covering the wing membrane of Protoperlaria as microtrichia; he considered the macrotrichia to be restricted to the veins. This interpretation now appears to be open to question. A careful comparison of these "microtrichia" (Fig. 8) with the macrotrichia of *Sialis* (Fig. 7) discloses that these structures possess several features in common:

a. Their size is approximately the same.

b. In *Lemmatophora,* all the setae, whether on the veins or on the membrane, appear to have a definite basal socket, as do those of *Sialis*. These are distinguishable even in Tillyard's photograph of the wing surface (1928a, Fig. 7).

c. On the hind wing of both *Sialis* and *Lemmatophora*, these hairs are distributed similarly, on the apical part of the costal cell, the stigmatic area, the wing tip, and in rows along the anterior longitudinal



Figures 9-11.

Figure 9A. *Lemmatophora typa*. Reconstructed cross section of posterior wing. Figure 9B. *Sialis mohri*. Cross section of posterior wing. Figure 10. *Taeniopteryx* sp. Ventral view of thorax showing presence of weak sternocoxal articulations. Figure 11. *Sialis mohri*. Ventrolateral view of thorax, showing sternocoxal articulations, structure of internal skeleton, and general resemblance to *Taeniopteryx*.

veins only. There is a decrease in size toward the base of the wing.

In attempting to differentiate between the setae on the veins and those on the membrane, Tillyard greatly overemphasized in his discussion the larger size of the setae on the costa and other veins. While it is true that the costal setae are very slightly larger than those of the membrane, much of the apparent size difference is illusory; in the fossil the setae of the wing membrane, seen against a colorless background, look brown, while those on the veins, seen against a brown background, look black, and therefore heavier.

Even though some size difference exists, this is not in itself sufficient reason for interpreting the hairs on the veins as macrotrichia, and those on the membrane as microtrichia, for in *Sialis* there is a similar size difference.

Furthermore, the microtrichia of *Sialis* (indicated by stippling in Figure 7, and shown in more detail in Figure 6) are very small, about the same size as the grain of the matrix in which are imbedded the fossils. Even were similar microtrichia present in *Lemmatophora*, as was almost certainly the case, they would therefore be obscured by the grain of the rock.

Tillyard's reluctance to recognize the macrotrichia on the wing membrane of *Lemmatophora* as such was probably due to an impression that macrotrichia do not occur in this location among the Exopterygota. While this is generally true, there is at least one exception. Since the Plecoptera are considered to be descended from the Protoperlaria, an examination was made of the wing surface of a representative of this order, *Pteronarcys californica* Newport. In this insect, prominent microtrichia are scattered over the entire wing. Small macrotrichia are sparsely distributed on the veins of the fore wing. But on the anal fan of the hind wing near the margin, large macrotrichia occur not only on the veins, but also on the wing membrane (Fig. 5).

From the above evidence, it seems reasonable to conclude that macrotrichia were present on both the veins and the wing membrane of the Protoperlaria, in size and distribution almost identical to those of *Sialis.*

D. THE THORAX.

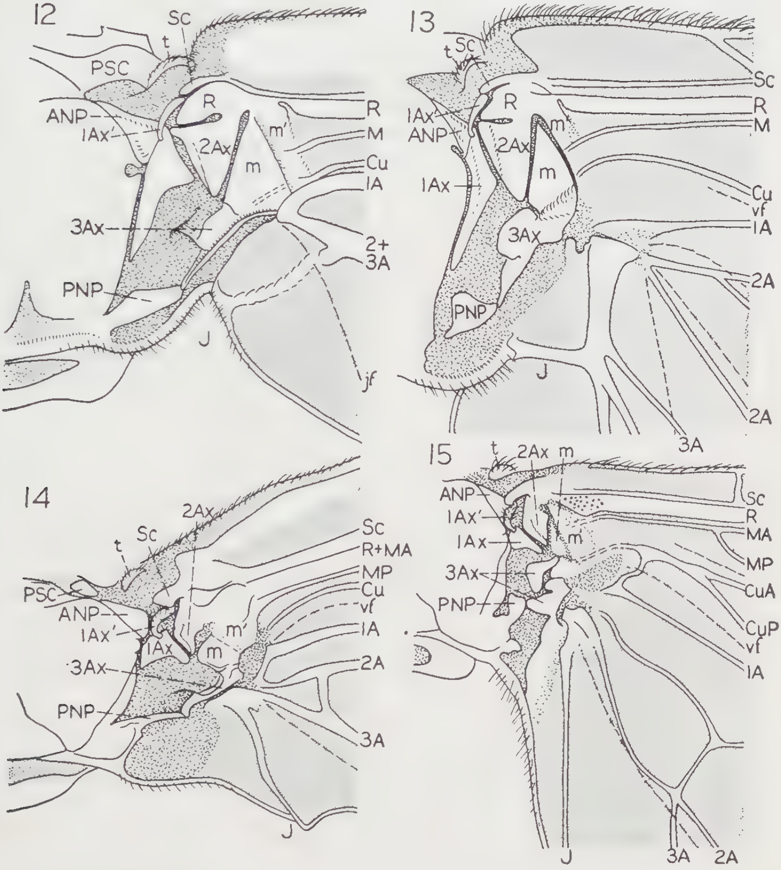
The sternum of the endopterygote thorax differs from that of the primitive Exopterygota in having a reduced furcasternum. The coxae of the Endopterygota have acquired a third point of articulation, on the furcasternum.

In the Plecoptera, the sternum is highly variable. Most studies of the thorax in this order have been made of *Pteronarcys,* or the large perlidae. In these stoneflies, the sternum is large and broad, and has slight resemblance to that of *Sialis.* But in some of the smaller stoneflies, such as *Taeniopteryx,* this is not the case.

The furcasternum (Fs) of *Taeniopteryx* (Fig. 10) is small, about the size as is that of *Sialis.* On both the mesothorax and metathorax, it bears on each side a process which extends close to the coxa; these have been termed *furcasternal arms* by Hanson (1946), who states "Although they are not articulated with the coxae, they appear to be adapted to offer them very strong support in the movement of the legs." The sternal coxal articulation (ST-CX ART) of the neuropteroid thorax is probably its most distinctive feature; one would expect this condition to have been derived from exactly such a stage as occurs in some stoneflies, by gradual strengthening of the association of the coxa and furcasternum. Once a sternal coxal articulation had become established, the thorax could be greatly strengthened by an infolding along the midline, reducing the exposed area of the furcasternum, so that the coxal bases become nearly contiguous. That such an infolding has taken place is indicated, not only by the structure of the furcasternum of neuropteroids, but also by the median longitudinal sutures on the basisterna (Fig. 11).

It is not necessarily to be inferred from the close resemblance of the thorax of *Taeniopteryx* to that of *Sialis,* that taeniopterygids are more primitive or more closely related to the Endopterygota than are other stoneflies. It is apparent, though, that these thoraces are constructed on the same general plan, and show remarkably similar capabilities for structural modification.

It is interesting to note, while reference is being made to the figure of the thoracic sterna of *Taeniopteryx*, the occurrence of openings of coxal glands (CxGl) on membranous areas of each coxa. Similar membranous areas occur on the hind coxae of *Sialis*, *Neohermes*, *Corydalus*, and *Chauliodes*, but in none of these insects has it been possi-



Figures 12-15.

Figure 12. *Pteronarcys californica* (Plecoptera). Base of right anterior wing. Figure 13. *P. californica*. Base of posterior wing. Figure 14. *Neohermes californicus* (Walk.) (Megaloptera). Base of anterior wing. Figure 15. *N. californicus*. Base of posterior wing.

ble to demonstrate by gross dissection any associated glandular structure. There is frequently, however, a small papilliform projection from one coxa interlocking with the membranous area of the other, apparently serving to restrict movement of the hind coxae.

E. WING ARTICULATION.

The axillary sclerites of Plecoptera (*Pteronarcys*, Figs. 12-13) and Megaloptera (*Neohermes*, Figs. 14-15) resemble each other in relatively large size, simple shape, and light degree of sclerotization. The wing base of *Pteronarcys* is the more generalized, while that of *Neohermes* appears to be modified for greater strength and flexibility. Only a few simple changes would be necessary to derive the more specialized wing base of *Neohermes* from that of *Pteronarcys*.

In *Neohermes*, the long posterior arm of the first axillary has been lost, and the anterior arm, which is connected to the basal process of Sc, is strengthened. The head of R has disappeared; this structure appears to be non-functional in *Pteronarcys*, and the articulation stronger without it. The third axillaries of the anterior wing are similar, but there has been a shift in the axis of articulation of the median plate with the second axillary, in *Neohermes*. In the anterior wing of both *Neohermes* and *Pteronarcys*, the third axillary articulates on a long, slender posterior notal wing process. In the posterior wing, however, the structures of third axillary and posterior notal wing process differ greatly. In *Neohermes* the third axillary is dissected, the median plate, flexor muscle attachment, and posterior articulating portion being separate. This condition, however, is not typical of all Neuroptera. It is also most unusual for the posterior wing process to remain attached to the metanotum; in nearly all other Neuroptera it is a separate sclerite, as in *Pteronarcys*.

The difference in articulation of the posterior wing may be due in large part to suppression of the anal fan in the Neuroptera. In *Neohermes*, although a functional fan is still present, the number of veins is small, and this region of the wing bears little resemblance to that of *Pteronarcys*.

F. CONCLUSIONS.

Some evidence for a close relationship between the Protoperlaria and the Neuroptera has been discussed above. This evidence, summarized below, consists in part of distinctive wing characters which are shared by the archaic Sialidae and the Protoperlaria (a), and in part of some similarities between the Plecoptera (derivatives of the Protoperlaria) and the Neuroptera (b). To these may be added some general characters which would of necessity be expressed in any group ancestral to the Endopterygota (c).

a. Distinctive common features of the protoperlarian and sialid wing are:

1. The density and arrangement of veins and cross-veins is about the same; in particular, Rs has usually only one or two branches.
2. There is a strong tendency for coalescence of MA and Rs.
3. The stem of MP is weak.
4. CuA of the hind wing of Protoperlaria is structurally similar to that of *Sialis,* the upper surface being deeply grooved.
5. The distribution of macrotrichia on the membrane and veins is about the same.

b. Features shared by the Plecoptera and Neuroptera, indicative of relationship are:

6. Furcasternum with a coxal articulation.
7. Generally similar shape and arrangement of axillary sclerites.

c. Other features of the Protoperlaria which are not so distinctive, but which are consistent with their probable role as ancestors of the Endopterygota are:

8. A well-developed anal fan.
9. Cerci
10. Ovipositor.
11. Tibial spurs, present not only at the apex, but in a series along the length of the tibia.
12. Five-segmented tarsi.

In addition to the above morphological evidence, a close relationship of the Protoperlaria and the Neuroptera is in agreement with recent theoretical work on the origin of the larva, and the significance of the pupal stage. The nymphs of the Protoperlaria were described in detail by Carpenter (1935); they appear to have been similar to those of the Plecoptera. Presumably, there was a large number of nymphal instars, as is the case in the Plecoptera, some species of which have more than thirty.

Bradley (1942) recognized the significance of the Protoperlaria, suggesting them as possible ancestors of the Endopterygota because they are the most generalized known Neoptera, and because of some similarities in development of their close relatives, the Plecoptera, and of *Sialis*. More recently, Sharov (1953, 1957) has developed a theory of the origin of holometabolous development from an insect with a large number of immature stadia, including both larval and nymphal stages, and with several imaginal instars. Of the living Neoptera, the Plecoptera, with their large number of immature stages, approach closest to this condition.

The evidence described above appears sufficient to justify the statement that a close relationship probably exists between the Protoperlaria and the Neuroptera; moreover, there is no known feature of the Protoperlaria which would prevent their being considered directly ancestral to the Endopterygota.

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LETTERING USED IN FIGURES

1A, 2A, 3A — first, second, and third anal veins.
ANEPS — anepisternum
ANP — anterior notal wing process
1Ax′ — anterior arm of first axillary sclerite
b — basal piece of media anterior
BA — basalare
C — costa
CuA — cubitus anterior
CuP — cubitus posterior
Cx — coxa
CxGl — membranous area bearing opening of coxal gland
EPM — epimeron
EPS — episternum
Fs — furcasternum
J — jugal vein
jf — jugal fold
KATEPS — katepisternum
m.m′ — medial plates
MA — media anterior
MP — media posterior
N1 — pronotum
PLC — pleural cleft
PLS — pleural suture
PNP — posterior notal wing process
PSC — prescutum
PWP — posterior notal wing process
R1 — anterior branch of radius
Rs — radial sector
SA — subalare
SC — subcosta
SP — spiracle
Ss — spinasternum
STA — sternal apophysis
ST-CX ART — sterno-coxal articulation
t — tegula
TN — trochantin
TR — trochanter
vf — vannal fold

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